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ECOLOGICAL ANALYSIS OF SPATIAL AND TEMPORAL PATTERNS OF PELAGIC ECOSYSTEM COMPONENTS POTENTIALLY INTERACTING WITH AN OTEC PLANT NEAR PUNTA TUNA, PUERTO RICO

ZOOPLANKTON CHARACTERISTICS

FINAL REPORT

Submitted to:

DOE/OHER

J.M. López and L.J. Tilly
Editors
Center for Energy and Environment Research
University of Puerto Rico
College Station
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FOREWORD

This document is part of the final report for the Department of Energy Project under Contract No. DE-AC05-76OR01833, which includes five main sections: Physical Characterization, Plankton, Primary Productivity, Chemical Characterization, and Summary and Synthesis. The document is primarily organized as a collection of preprints of articles being submitted for journal publication. Once all sections are completed, the entire series will be combined as a five chapter volume dealing with the environmental aspects of the siting, construction and operation of an Ocean Thermal Energy Conversion Plant based off the south coast of Puerto Rico. Of prime concern in these studies, as suggested by the title, is the relationship among the scale of distribution of natural phenomena, the scientific detectability of pattern, and the alterations of pattern likely to be caused by the hypothetical 100 MWe power plant adopted as the design unit.

SPATIAL AND TEMPORAL VARIATIONS OF OCEANIC ZOOPLANKTON NEAR PUERTO RICO

Final Report

Submitted to:

DOE/OHER

by

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ABSTRACT

Diel and bimonthly variations in horizontal distributions of selected zooplankton higher taxa and species were followed within the upper 100 meters off the south coast of Puerto Rico during 1980. Spatial pattern examined encompassed scales of kilometers to hundreds of kilometers. A series of oblique tows with 0.75 m diameter, 202 u mesh nets were taken to estimate zooplankton abundances and hydrocasts made for measures of a number of habitat variables.

Analysis of sampling variability relative to scale revealed a general lack of pattern associated with spatial scales larger than several kilometers. A statistically significant seasonal variability component was detected in most zooplankton categories. Maximum abundances occurred in July. The observed seasonal pattern is compatible with the hypothesis that the forcing mechanism driving seasonality is input of nutrients into euphotic zone by upwelling along the periphery of large, low salinity lenses of surface water passing through the region.

INTRODUCTION

Ecological processes organizing zooplankton communities affect and are affected by the spatial and temporal patterns shown by individuals and species. For this reason, the quantitative description of pattern is of fundamental importance in marine ecology. This pattern can arise from a variety of causal mechanisms (Stavn, 1971) and is expressed over wide spatial and temporal scales (Cassie, 1963; Star and Mullin, 1981; Fasham et al., 1974; Wiebe et al., 1976; Bernal, 1981 and Johnson and Briton, 1963). The association of pattern over a range of spatial and temporal scales with characteristic environmental processes are reviewed by Haurey et al. (1978). They define six classes within a spatial continuum from 1 cm to 10^4 km, mega-scale (>3000km) macro-scale (1000 to 3000km), meso-scale (100 to 1000 km) coarse scale (1 to 100 km), fine (1 to 1000m) micro-scale (<1m).

The purpose of this paper is to describe horizontal patterns of abundance within the intermediate spatial scales (fine, coarse and meso-scale) for some zooplankton components in the surface waters south of Puerto Rico and to discuss temporal variation in this pattern relative to several parameterizations of the environment, viz salinity, temperature, oxygen and chlorophyll.

The major physical features of the eastern Caribbean are well-known and have recently been reviewed by Nowlin and Morrison (1982). The survey area lies in the northeast corner of the Venezuela Basin. Surface flow in this region is complex, but the mean flow is to the west (Metcalf, 1976; and Fornshell, 1981). The upper 30 to 90 m of water with salinities generally below

36.5%, Caribbean Surface Water, has its origin in the North Equatorial and Guiana Current systems. It is formed from a mixture of these waters and large inputs of Amazon and Orinoco River water, carried into this region by prevailing winds and currents (Nowlin and Morrison, 1982; Froelich *et al*., 1977).

Seasonal variation in the depth of the mixed layer ranged from 90 meters in January to 30 m in September. Internal waves, oscillating with a period approximating a semi-diurnal tide, can cause diel variations of 20 to 30 m in the depth of the upper layer (Fornshell and Capella, 1982).

Below the Caribbean Surface Waters lies the Subtropical Underwater. Extending down to approximately 200 m, it is characterized by a salinity maximum >37‰, located at around 125 m. This water has its origin in the surface waters of the North Atlantic central gyre, and moves into the survey region through the Jungfern-Anegada Passage (Nowlin and Morrison, 1982).

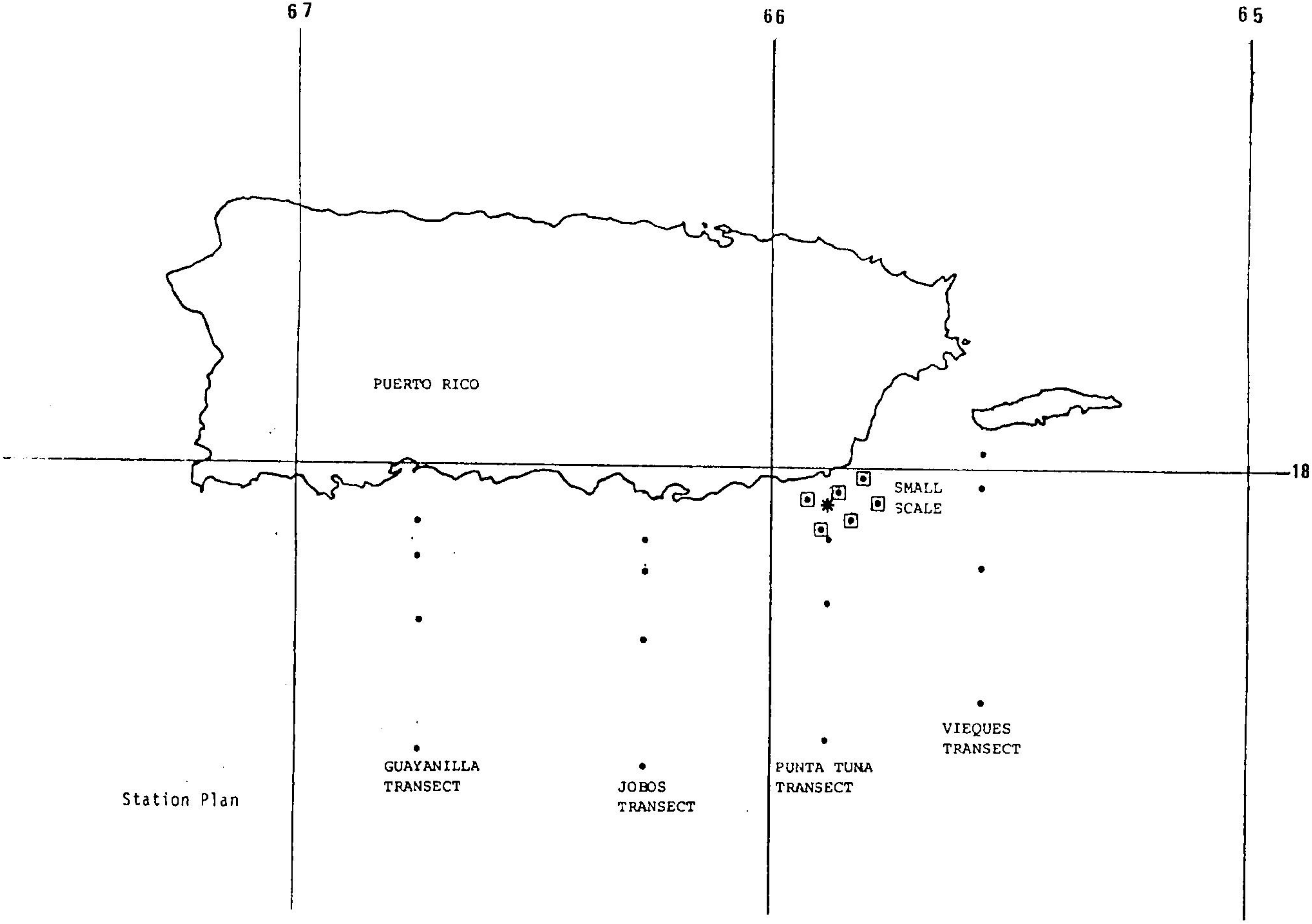
Seasonal variations in nutrients, salinity, temperature and oxygen are confined to these two upper layers. Values of phosphate-P, nitrate/nitrite-N and ammonium-N are near the minimum levels of detection throughout the year in the upper 100 meters. The nutriocline starts at depths between 120 and 150 meters near the base of the Subtropical Underwater.

METHODS

Sampling: Bimonthly collections of zooplankton and auxiliary environmental data were carried out between January and November, 1980 within a 7.5×10^3 km ^{2} area south of Puerto Rico. The zooplankton were sampled with 0.75 m diameter, opening and closing nets of 202 u mesh. Oblique tows were taken through the upper 100 m of the water column, a zone which encompasses the total vertical extent of the Caribbean Surface Water and varying portions of the Subtropical Underwater. An average tow trailed a linear distance of approximately 1 km and filtered 377 m^3 of water. Details of methods, times, and locations of sampling are available elsewhere (CEER, 1980 a-f). A brief description of the sampling design is presented here.

Zooplankton distribution patterns were investigated on three different horizontal spatial scales (Fig. 1). Within station variability was assessed from a three tow day/night replicate series taken within a 24 hr period at a site (Benchmark) 5 km SE of Puerto Rico (17° 56.3' N, 65° 51.5' W). Collections were made within a 1.5 km radius of this position, a spatial scale roughly corresponding to the "fine" pattern of Haurey et al. (1978). A series of day/night samples was also taken within a three by two station grid (coarse scale grid) with inter-station distances of 6.4 km. The six stations of the coarse grid bracketed the Benchmark site. Mesoscale pattern was examined within a grid consisting of four north-south station transects spaced 50 km apart (65° 30' W to 66° 48' W). Each transect contained four stations located from 5 km to 50 km offshore.

Hydrocasts with 5ℓ or 12ℓ Niskin bottles were made to a depth of 1000 m at most stations for calculation of the baroclinic flow pattern within the survey region. Water samples from these casts were used for measurements of salinity, oxygen, and chlorophyll a. Continuous temperature profiles were made through the upper 100 meters. These were supplemented by



Station Plan

temperature measurements with paired reversing thermometers from the hydrocasts.

Data Analysis. The 196 samples taken during the survey have been analyzed for total zooplankton biomass, total copepods, total larvaceans, total chaetognaths, and the copepod species *Clausocalanus furcatus*, *Paracalanus* cf *parvus*, *Calocalanus pavo*, and *Oithona plumifera*.

The species selected for analysis are frequent and abundant within the study area. Literature review indicates that their vertical populations distribution centers are, generally, located within the upper 100 m (e.g., Moore and O'Berry, 1957; Michael and Foyo, 1976; McGowan and Walker, 1979; Roe, 1972; and Zoppi, 1961).

Zooplankton biomass was measured using a volume displacement method (Ahlstrom and Thrailkill, 1963). Subsamples for zooplankton were taken with a Stempel pipette after the contents of a sample had been randomly distributed by a series of stirrings and back stirrings. Replicate determinations of biomass measurements and zooplankton counts were not more variable than expected from a random (Poisson) distribution. Relevant information on subsample size and error estimates is summarized in Table 1. Examination of within station variability indicates that the counting error is small relative to the field sampling error.

Within each sampling scale analysis of variance procedures (ANOVA) were used to determine variance components associated with seasonal and, when appropriate, station position, day/night,

TABLE 1. Theoretical coefficients of variation (σ/μ x 100) for zooplankton components based on mean counts per subsample.

	Biomass	Copepods	Larvaceans	Chaetonaths	C. furcatus	P cf parvus	C.pavo	O.plumifera
Total Samples	29	196	196	196	196	196	196	196
Mean Counts	-	393	69	23	81	11	10	47
Coefficient of Variation	3[+]	5	12	21	11	30	32	15

[+] Observed mean coefficient of variation in replicated biomass measurements of 29 samples.

and interaction effects. Preliminary analysis of the data revealed that sample variances were positively correlated with the mean. A log (X+1) transformation was performed to equalize the variances and normalize distributions. A procedure outlined by Steel and Torrie (1960) was used to correct for missing data points.

The variance components generated by the ANOVA testing were used in a hierarchial analysis of variance relative to spatial scale to determine intensity of pattern associated with different spatial scales (e.g., Grieg-Smith, 1964). In this analysis it is assumed that the sample variance attributable to a given spatial scale is superimposed on the variability observed within the smaller scales. Due to these added variance components overall variability should increase with increases in scale if characteristic patterns exist on those scale.

Correlations between the environmental parameters and zooplankton spatial patterns were determined using the variance components associated with the within cruise spatial and the bimonthly temporal scales. Relationship between pairs of variables were expressed as covariances and correlation coefficients (r) calculated from the following formulae:

$$\mathrm{var}\ (x+y) = \mathrm{var}\ (x) + \mathrm{var}\ (y) + 2\ \mathrm{Cov}\ (x,y)$$

$$r = {}^{\mathrm{Cov}\ (x,y)}/[\mathrm{Var}(x)\ \times\ \mathrm{Var}(y)]^{1/2}$$

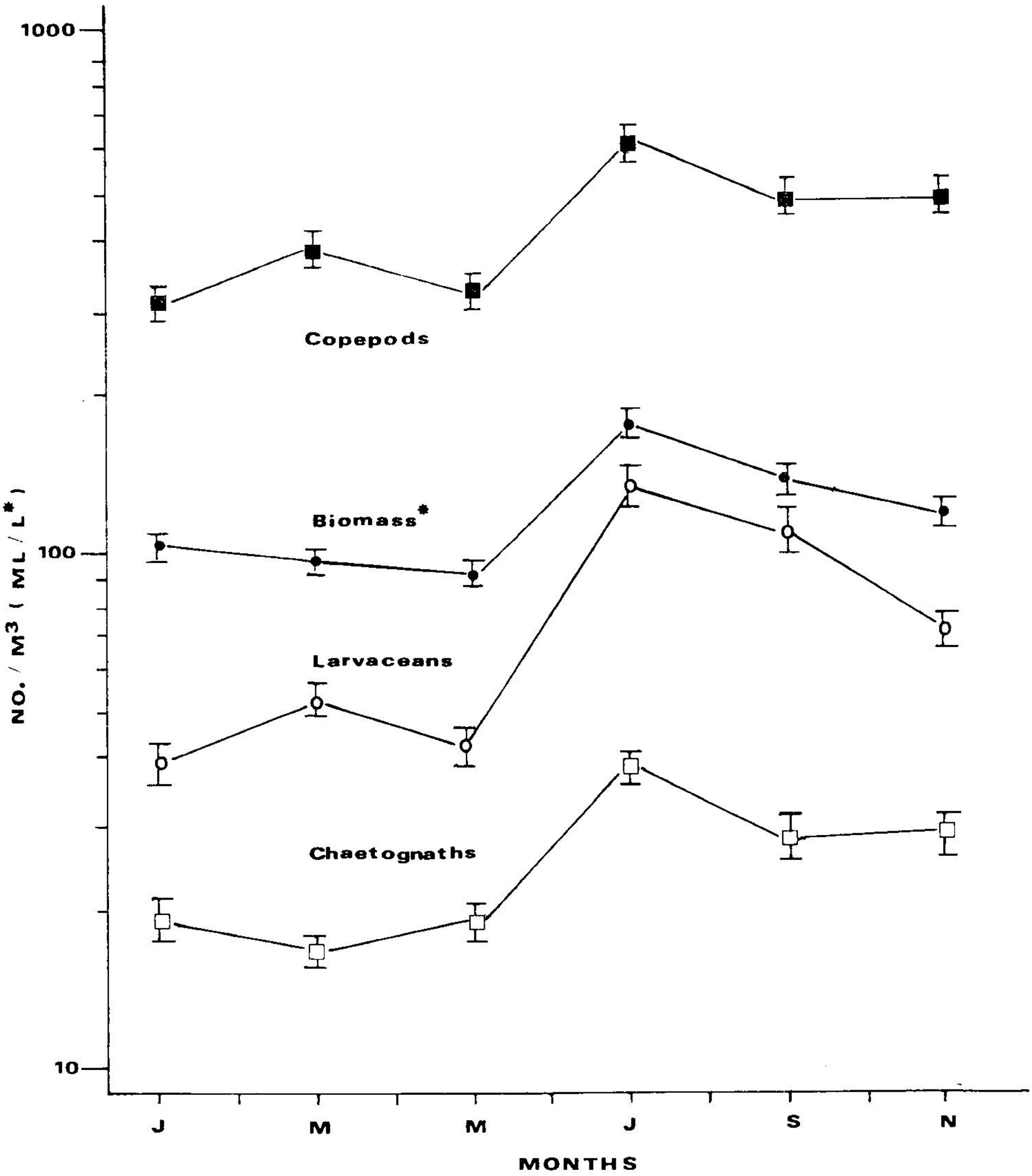
where x and y represent zooplankton data and environmental variables, respectively, (Kershaw, 1960). Data used in this analysis were largely derived from the coarse and mesoscale grids since hydrocast for estimation of habitat variables and net tows at Benchmark were not taken concurrently. The additional parametric and non-parametric procedures used are described in standard statistics texts (e.g., Tate and Clelland, 1954; Sokal and Rohlf, 1968).

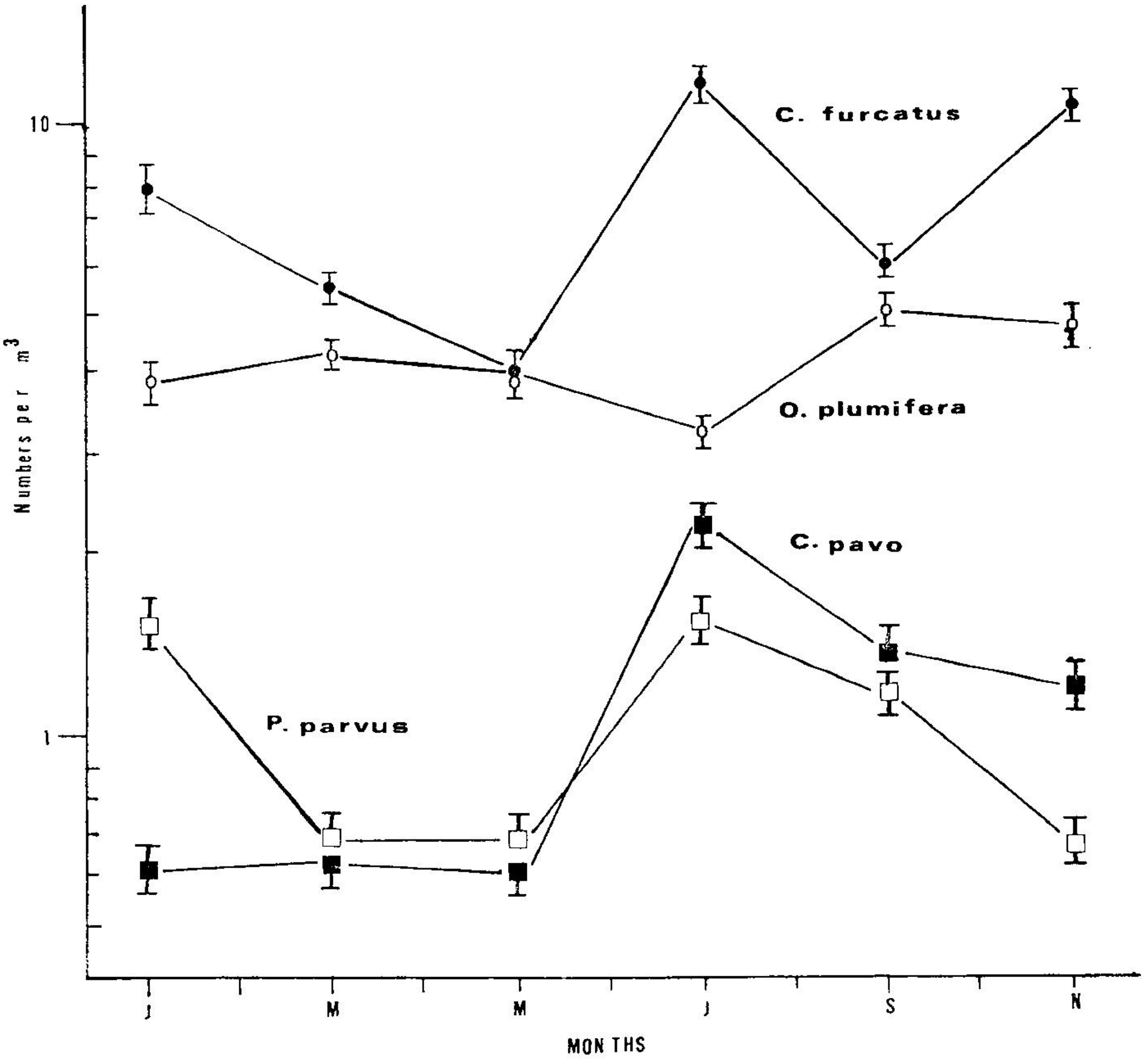
RESULTS

Temporal Effects: Mean abundances per sampling event for the seven zooplankton categories are shown in Figs. 2 & 3. The results of the anova testing for this set of data are found in Table 2. Although some caution should be exercised in interpreting these results, due to the potential for multiple testing effects, several trends are apparent. (If an individual ANOVA probability for an "alpha" error $p \leq 0.001$ is accepted, the "survey wide" significance level is $p \leq 0.02$).

All categories showed either non-significant ($P \leq 0.05$) or inconsistent day/night variations in abundance. There is no large variability component which can be associated with mass vertical migration. Excluding Oithona plumifera significant seasonal differences ($p \leq 0.001$) were observed over all spatial scales in most zooplankton categories (Table 2).

It is possible that the significant "temporal" variability is a artifact produced by interactions of spatial pattern and temporal effects within a given sampling scale (i.e., the presence or absence of fine scale patchiness at benchmark during a particular sampling episode) rather than "true" bimonthly temporal variations. To assess the possibility of this effect having occurred, the agreement in bimonthly abundances among the three sampling scales was examined for each zooplankton category using Kendall's concordance test. Significant positive


1000
100
10
NO. / M3 (ML / L*)
Copepods
Biomass*
Larvaceans
Chaetognaths
J
M
M
J
S
N
MONTHS



C. furcatus
O. plumifera
C. pavo
P. parvus
Numbers per m3
10
1
J
M
M
J
S
N
MONTHS

TABLE 2. Analysis of variance of zooplankton components (*=p< .05, **=p< .01, ***=p< .001).

	Source	df	Biomass Mean Square	Copepods Mean Square	Larvaceans Mean Square	Chaetognaths Mean Square	*C. furcatus* Mean Square	*P.* cf *parvus* Mean Square	*C. pavo* Mean Square	*O.plumifera* Mean Square
Fine Scale (Benchmark)	Months	5	.0885***	.1240***	.4821***	.2610***	.2043**	.126	.328***	.0756
	Day/Night	1	.0578	.9476***	.0059	.0231	.0126	.0126	.0823	.3405
	Day/Night:Month Interaction	5	.0151	.0072	.0382	.0658	.1239	.0130	.1181	.0705
	Error	23	.0117	.0051	.0251	.0361	.0411	.0905	.0530	.0384
Course Scale	Months	5	.1650***	.1926***	.7131***	.3486***	.5119***	.5347***	.7550***	.0959
	Day/Night	1	.0005	.0254	.1153	.2782	.3230	.0139	.0004	.1376
	Day/Night:Month Interaction	5	.0107	.0050	.0235	.0270***	.0390	.0823	.0187	.0156
	Error	56	.0081	.0145	.0432	.0296	.0351	.0373	.0711	.0408
Meso Scale	Months	5	.0694**	.2145***	.6499***	.1725***	.531***	.6368***	1.0025***	.2031***
	Station	15	.0282	.0177	.1232**	.0782**	.0447	.0527	.0680	.0457
	Error	72	.0202	.0110	.0474	.0353	.0464	.0632	.0285	.0285

concordance was observed ($p \leq 0.01$) within the six zooplankton categories having significance between cruise variation. *Oithona plumifera* was inconsistent in regard to spatial scale in its within cruise response. Since concordance is most easily explained by assuming similar changes in background this result constitutes circumstantial evidence for true temporal changes in abundance between cruise periods.

Kendall's concordance method was also used to examine similarity in seasonal abundance trends within the groups showing within cruise concordance between the spatial scales. The sums of the ranks over the three spatial scales for each cruise from the preceding concordance test were used to rank each cruise and the Kendall's concordance test reapplied. Zooplankton biomass and total copepods were omitted from this analysis since these groups have as components all or some of the remaining entities. There was significant agreement ($p \leq 0.05$) among the remaining categories suggesting that zooplankton responds similarly to bimonthly changes within the study area. Student-Newmann-Keuls multiple range tests showed that densities tended to be higher for most categories in the sampling period after the surface salinity drop, July to November, with significantly higher abundances occurring in July. The size of the annual fluctuations were low. Ranges in the mean bimonthly abundances varied from 3x for most higher taxa categories to 10x for *C pavo*, an amplitude roughly equivalent to the range in sampling variability within a cruise.

Spatial Effects: Significant station effects within a spatial scale were interpreted as an indication of stable pattern at that level (Lewis, 1978). Within the mesoscale grid significant station effects were observed for total larvaceans and total chaetognaths (Table 2). A. posteriori examination of these results using the Student-Neuman-Keuls procedure showed that the significance originated from higher abundances at the inshore stations on the two westernmost transects. In a companion study run concurrently with this survey a series of samples were taken from the insular shelf out to 2.5 km. These nearshore samples showed consistently higher biomass and abundance levels (CEER, 1980 a-f). At the inshore terminus of the western transects this zone of higher abundances appears to have been shifted offshore due to a broadening of the shelf and possible outwelling effects from two nearby bays. The higher abundances of larvaceans and chaetognaths in this region is a reflection of an abundance gradient associated with an "island mass effect" rather than a stable mosaic within the survey area (Jones, 1962; Sanders and Stevens, 1973; Gilmartin, 1974).

Lack of significant station effects for a zooplankton category within a spatial scale does not, in itself, imply a lack of characteristic spatial pattern only the lack of stable structure. Temporary pattern (ephemeral pattern due to spatial-temporal interactions) could still be present (Lewis, 1978). To test for the existence of ephemeral pattern the sums of the squares and degrees of freedom for the day/night effects and cruise-day/night interaction effects for the Benchmark site and the coarse scale grid were added to their respective error sum of squares. The same procedure was carried out for the station effect sum of squares and degrees of freedom within the mesoscale grid. In most instances this involved a pooling of non-significant mean squares. Error mean squares were then recalculated (Table 3). Assuming that the error mean square at the Benchmark site is an unbiased estimate of fine scale variability, increases in error mean square within coarse and mesoscale grids would be attributable to the added effects of their stable and ephemeral pattern. No general trend in variability is evident. Increasing distances between samples are not accompanied by the introduction of any statistically detectable variance components that would be associated with larger scale pattern.

Excessively large fine scale sampling variability can produce a result that would be wrongly interpreted as a lack of larger scale pattern by overwhelming the larger pattern variance components in a hierarchal analysis of variance. Antilogs of the square root of the mean squares at the Benchmark site (Table 2) can be used as an estimate of sampling variability at a given site and time. Expressed on a proportional bases to their respective means, these values ranged from 1.18 X (total copepods) to 2.00X (Paracalanus cf parvus). This range is within the sampling variability in the literature values reported for net caught zooplankton observed in similar studies (Wiebe, 1971). The lack of larger spatial pattern doesn't appear to be a statistical artifact.

It seems that the oceanic environment off Puerto Rico is relatively uniform over the coarse and mesoscales examined in the

TABLE 3. Spatial sampling variability (error mean square) in $\log_{10}$ at fine scale, coarse scale, and meso scale stations. Significance relative to fine scale (*$p<0.05$;** $p\leq0.01$).

	FINE SCALE MEAN SQUARE	COARSE SCALE MEAN SQUARE	MESO SCALE MEAN SQUARE
Biomass	.0139	.0089	.0202
Total Copepods	.0073	.0139*	.0122
Total Larvaceans	.0267	.0428	.0605**
Total Chaetognaths	.0407	.0316	.0427
Clausocalanus furcatus	.0541	.0401	.0461
Paracalanus cf *parvus*	.0745	.0405	.0614
Calocalanus pavo	.0681	.0656	.0718
Oithona plumifera	.0544	.0403	.0314

sense that little characteristic pattern, stable or ephemeral, is associated with these spatial scales.

Environmental Correlates: Cruise averages for the environmental parameters measured (temperature, salinity, oxygen, and chlorophyll a) are plotted in Fig. 4. Maximum surface salinities were observed during March and May. Surface salinities dropped in July reaching a minimum in September. The observed seasonal variation follows the reported pattern for this region and is related to precipitation and Amazon-Orinco River discharge within the Caribbean Surface Waters source regions rather than local runoff and precipitation (Froelich et al, 1978). Surface temperatures seasonal trends oppose surface salinities with minimum values recorded in February and maximum temperatures in September. Dissolved oxygen values are highest in the January and March cruises, a reflection of the lower surface temperatures during this period. A sub-surface oxygen maximum around 75 meters was present during the May, July, and September cruises. This maximum was associated with a chlorophyll maximum and generally below the thermocline. The chlorophyll a seasonal maximum occurred in July. Relatively high values were also seen during the January and September cruises.

In general, little correlation was found between the abundances of the eight zooplankton categories and habitat variables. Among and within cruise correlations are listed in Table 4. Working at an overall significant level of $p \leq 0.06$, two zooplankton categories showed significant correlations, zooplankton biomass with chlorophyll a on a seasonal basis and C. pavo with salinity and temperature on a within cruise basis. The

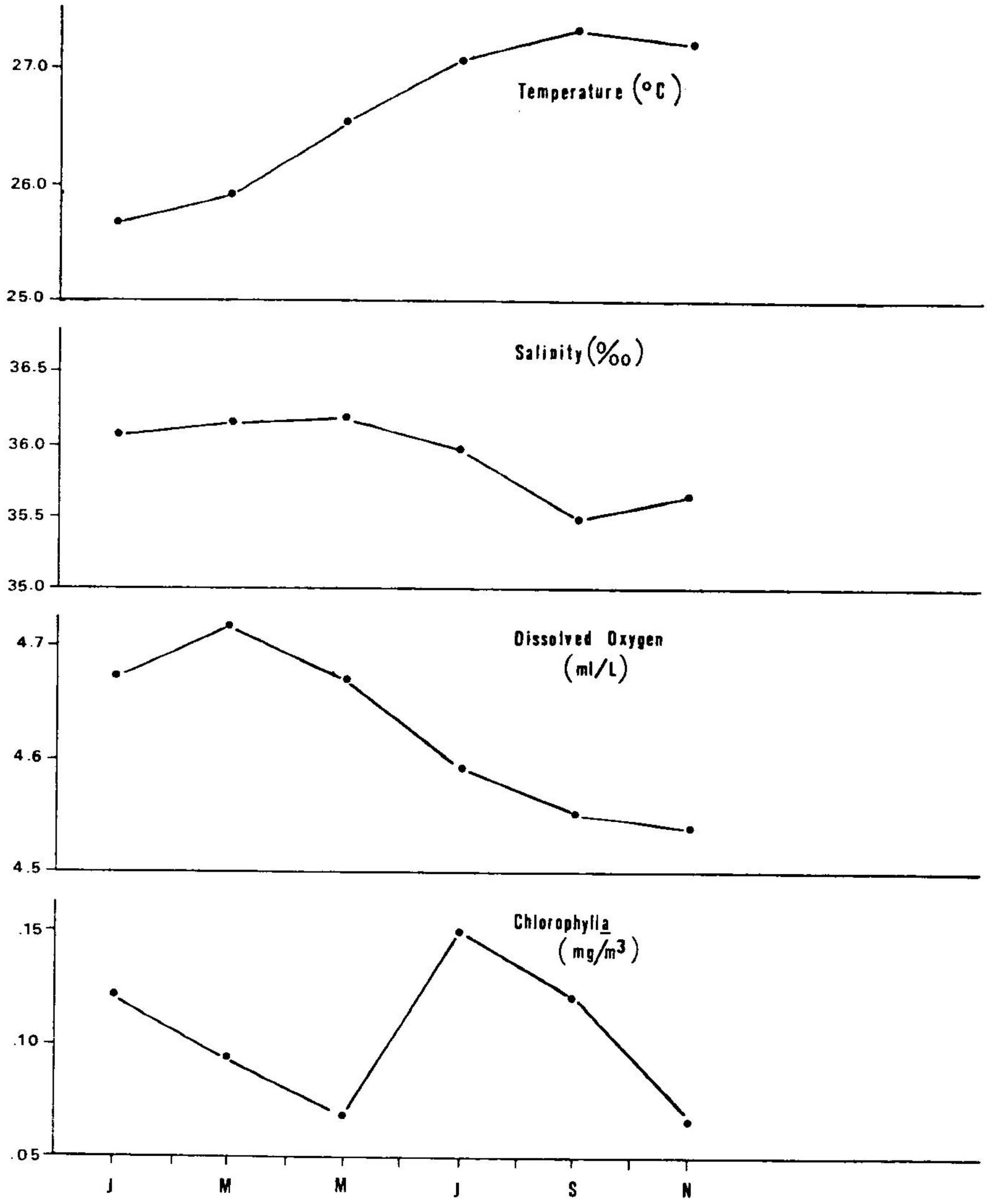

27.0
26.0
25.0
Temperature (°C)
36.5
36.0
35.5
35.0
Salinity (‰)
4.7
4.6
4.5
Dissolved Oxygen (ml/L)
.15
.10
.05
Chlorophyll a (mg/m3)
J
M
M
J
S
N

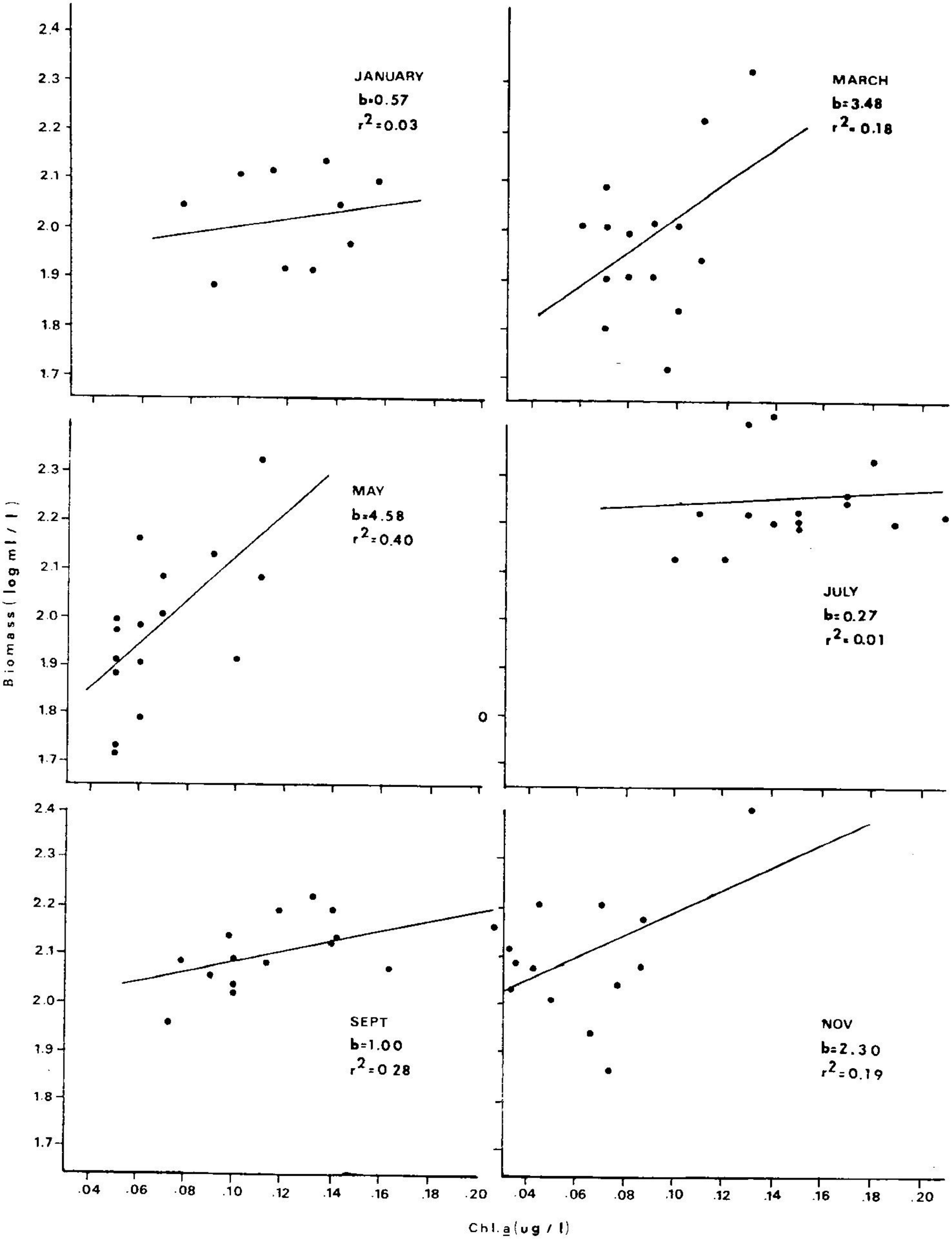
TABLE 4. Correlation coefficient within and between cruises of zooplankton components and hydrocast data. (*$p \leq 0.10$; **$p \leq 0.05$; and ***$p \leq 0.01$)

	Chlorophyll		Temperature		Salinity		Oxygen	
	Between	Within	Between	Within	Between	Within	Between	Within
Biomass	+.810*	+.326***	+.591	-.0008	-.638	-.106	-.694	-.082
Copepods	+.500	+.179*	+.734	-.059	-.635	-.039	-.788	-.041
Larvaceans	+.664	+.130	+.741	-.159	-.751	-.035	-.765	+.027
Chaetognaths	+.568	+.212*	+.635	-.029	-.603	-.044	-.765	-.010
C. furcatus	+.760	+189*	+.413	-.178	-.603	-.098	-.674	+.051
P. cf *parvus*	+.989**	+.059	+.294	+.151	-.405	-.215	-.360	+.120
C. pavo	+.621	+.087	+.753	+.339***	-.724	-.333***	-.838*	-.190*
O. plumifera	-.383	+.110	+.304	+.168	-.510	-.076	-.401	-.122

tendencies toward negative correlations with salinity and oxygen and positive correlations with temperature among cruises reflects the dichotomy in abundances between high and low surface salinity periods. A more interesting relationship in terms of a possible direct cause-effect interaction is the positive correlation between most zooplankton categories and chlorophyll a both on a among and within cruise basis. The relationship is most consistent and shows greatest significance between chlorophyll a and biomass. Individual cruise linear regressions of chlorophyll a on biomass showed that the relationship between the two varied with respect to both slope and explained variability, r^2 (Fig. 5). Higher slope values and less scatter are associated with cruises showing low mean chlorophyll a concentrations. The product-moment correlation coefficient between mean chlorophyll a concentrations and the slope of the regression lines was significant at the $p \leq 0.05$ level, and at the 0.10 level with r^2. In both respects, a closer coupling between phytoplankton and zooplankton is evident as the former decreases in abundance. Such an affect could develop if there existed a quasi-equilibrium between phytoplankton growth, zooplankton grazing and nutrient recycling that is periodically destroyed by the advective input of nutrients into the euphotic zone (Sharp et al., 1980).

DISCUSSION

Whether temporal variations such as those described in this study represent a "true" seasonality or short term haphazard variations caused by local biological or hydrographic conditions, has not been well-established for the eastern


JANUARY
b=0.57
r^2=0.03
MARCH
b=3.48
r^2=0.18
MAY
b=4.58
r^2=0.40
JULY
b=0.27
r^2=0.01
SEPT
b=1.00
r^2=0 28
NOV
b=2.30
r^2=0.19
Biomass (log ml / l)
2.4
2.3
2.2
2.1
2.0
1.9
1.8
1.7
0
.04
.06
.08
.10
.12
.14
.16
.18
.20
Chl.a(ug / l)

Caribbean (e.g., Calef and Grice, 1967; Beers _et al._, 1968; Lewis and Fish, 1969; Stevens, 1971; and Moore and Sanders, 1977). The uncertainty reflects both the lack of offshore studies with long term time series sampling ($\geq$2 yr.), and the size of sampling effort needed to detect the relatively small temporal variability observed. The duration of the present study is too short to address the problem of seasonality directly, but several characteristics of the temporal distribution of biomass and abundances suggest the zooplankton are responding to a strict seasonal cycle. Most zooplankton categories showed concordance in their seasonal pattern with highest abundances occurring in the summer. The nature of the coupling observed between phytoplankton (chlorophyll _a_) and zooplankton biomass fluctuations suggest that hydrographic conditions leading to nutrient enrichment within the euphotic zone underlie the observed variation in both groups. Within any cruise, a general agreement exists over all spatial scales sampled on environmental suitability as expressed in size of the plankton standing stocks. The forcing agent that produces between cruises variability appears to operate over large spatial scales affecting overall production rather than a few isolated components. This is consistent with the character of a true seasonal response.

Further evidence for regularly reoccurring variations of a seasonal nature of a more direct nature comes from other studies in the eastern Caribbean, and western tropical Atlantic. Nutt and Yeamen (1975) reported similar seasonal trends in total zooplankton biomass and abundance levels at their offshore station during a year's study of the north coast of Puerto Rico.

In Barbados, Lewis et al. (1962) and Kidd and Sanders (1979) also found higher summer zooplankton standing crops. Lewis and Fish (1969) reported higher summer densities in many zooplankton groups, but concluded that the temporal changes in abundance resulted from local hydrographic factors. In contrast, Moore and Sanders (1977) observed no strong evidence for strict seasonality. However, there is a noticeable trend in their data for large zooplankton fluctuations with higher peaks in late winter and summer. Elsewhere in the Caribbean, Calef and Grice (1967) found a threefold increase in zooplankton from winter to summer season off the northeast coast of South America.

Seasonality in the oligotrophic subtropical waters of the North Atlantic central gyre has been linked to the yearly migration of the thermocline with maximum phytoplankton followed by increases in zooplankton abundances occurring in the spring after nutrient enrichment by winter mixing of the surface waters to the depth of the permanent thermocline (Menzel and Ryther, 1960 and 1961; Deevey, 1971). This mechanism of nutrient enrichment may account for the relatively high chlorophyll a concentrations during the January cruise, but would not explain the high phytoplankton and zooplankton levels during the summer when the mixed layer is shoaling and vertical stability is at a maximum. Seasonal changes in the strength of the Caribbean current also occur which can generate hydrographic conditions leading to increased productivity. Geostrophic data from the six cruises show a definite bi-seasonality in the current field with flow from May through September characterized by the presence of eddies and strong meanders (Fornshell, 1981). Mean dynamic heights increased steadily during this period. Eddies of this type have been associated with regions of higher production elsewhere in the Caribbean (Ingham and Mahnken, 1967; Powles, 1976). The mesoscale variability observed is comparable to or incorporated within the mesoscale sampling grid. Increases in production due to mesoscale turbulence should ultimately be reflected in higher mesoscale zooplankton spatial variability. No evidence of this phenomenon was observed within our study area.

Lower salinities, indicating an increased presence of Amazon and Orinoco source water, have been associated with higher zooplankton abundances (Lewis *et al.*, 1962; Kidd and Sanders, 1979 and Calef and Grice, 1967). In this study no consistent correlation was observed between standing stocks within the various zooplankton categories and surface salinities. Peak abundances occurred at the initiation of the surface salinity shift, but declined thereafter while salinities continue to drop until September. This lack of correlation may reflect a nonlinear relationship between these factors. Ryther *et al.* (1967) found that the low salinity waters originating from the Amazon runoff generally contained low nutrient levels (silicate remained at relatively high levels) negating the possibility of direct nutrient enrichment from this source. They suggested that upwelling of nutrient-rich water at the periphery of large anticyclonic eddies ($\leq 33^{o}/_{oo}$ core diameters of 400 to 600 km) of low salinity water originating from Amazon runoff contributed to or cause the increase in plankton levels they observed. Kidd and

Sanders (1979) associated higher summer plankton standing stocks within the study area off Barbados with the nutrient enrichment that occurs as these low salinity "bubbles" move through the region. Maximum Amazon runoff occurs from May to June (Gibbs, 1970). Much of this outflow is diverted into the open ocean. Since surface waters from this region enter the eastern Caribbean it is likely that large lenses of Amazon water are transported into the Caribbean and contribute to the low salinity surface water which passes through this region during the summer (Gordon, 1967; Forbes-Ortega and Herrera, 1976; and Mazeiba _et_ _al_., 1980). Froelich _et_ _al_. (1979) reported that the first appearance of this low salinity water south of Puerto Rico occurs in the June-July period with minimum surface salinities occurring during the fall, which agrees with our observations. Upwelling associated with large, low salinity lenses as the forcing mechanism underlying the summer increases in plankton would be consistent with the peaks of chlorophyll _a_ and zooplankton occurring in July. If the lenses maintained their initial spatial integrity any upwelling which accompanied them would occur on scales beyond those which could be distinguished as distinct pattern by this study.

From the results of this study and others in the region, it seems clear that a true seasonal response occurs within the zooplankton assemblages in the eastern Caribbean. This variability doesn't appear to be the result of any instability within local hydrographic systems, but rather is forced by large scale physical changes affecting the whole of the eastern Caribbean. The question of the exact process or processes involved is yet to be resolved.

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THE MEASUREMENT OF ZOOPLANKTON PATCHINESS

Final Report

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Average abundance as well as the intensity of patchiness (degree of aggregation) influence the frequency of encounters among individuals in the plankton and, consequently, both factors play important roles in the dynamics of planktonic communities. Alternatively, differences between communities may be reflected by differences in abundances or patchiness of their component populations. For example, Star and Mullin (1981) inferred differences in habitat features of the nearshore and offshore plankton communities of the California Current from differences in the intensity of patchiness based on variance to mean ratios.

In this note we discuss some difficulties involved in the measurement of the intensity of patchiness (see Pielou, 1977 for a more general review). One of the more common and easily applied methods used in the analysis of spatial pattern is to measure the deviation of variability observed in a sample set from a random (Piosson) expectation by the use of various indices of aggregation. Although these indices have come under criticism from numerous authors (e.g., Fasham, 1978) they will probably see continued use given the sampling and analytical difficulties associated with the use of more sophisticated analytical techniques, i.e., spectral analysis or the empircial description of pattern. The variance to mean ratio, $S^2/\bar{X}$,

where: S^2 = sample variance, $\sum_{i=1}^{n} \underset{n-1}{(X_i - \bar{X})}/n$

$\bar{X}$ = the sample mean, $\sum_{i=1}^{n} X_i / n$

X_i = the number of individuals per sample

n = the number of samples

is one of the more frequently employed indices used to statistically describe pattern. Because of scaling effects, to be a valid measure of patchiness the $S^2/\bar{X}$ ratio must be calculated on individuals per sample basis rather than using values adjusted to some standard unit, i.e., $\#/m^3$. Index values less than, equal to, and greater than unity indicate even, random and patchy distributions, respectively.

Unfortunately, as previously noted, variance to mean ratios, and other related indices are subject to scaling effects which impair their usefulness as a comparative measure of the intensity of patchiness between sets of samples showing large differences in mean density (Morisita, 1959). For instance, given a set of values, x, and a constant multiplicative scaling effect, c, we find that:

$$\text{variance } (cx) = c^2 \text{variance } (x)$$

Thus, variance to mean ratios will vary directly with mean density, a feature commonly observed in plankton studies (e.g., Wiebe 1970). Also, factors underlying differences in mean abundance and patchiness can operate independently in nature and it would be desirable to obtain independent measures of both. The index used to measure the intensity of patchiness should ideally be insensitive to changes in the average number of individuals per sample. Lloyd's (1967) index of patchiness and the nearly equivalent Morisita's (1959) Index of Dispersion largely satisfy these criteria. Lloyd's index of patchiness is defined as the ratio of mean crowding to mean density, m^*/m, where: m^* (mean crowding) = mean density of individuals per sample per individual, $\sum_{i=1}^{n} Xi\ (Xi - 1)\ /N$

m = mean density per sample, $\sum_{i=1}^{n} Xi\ /n$

N = total number of individuals, $\sum_{i=1}^{n} Xi$

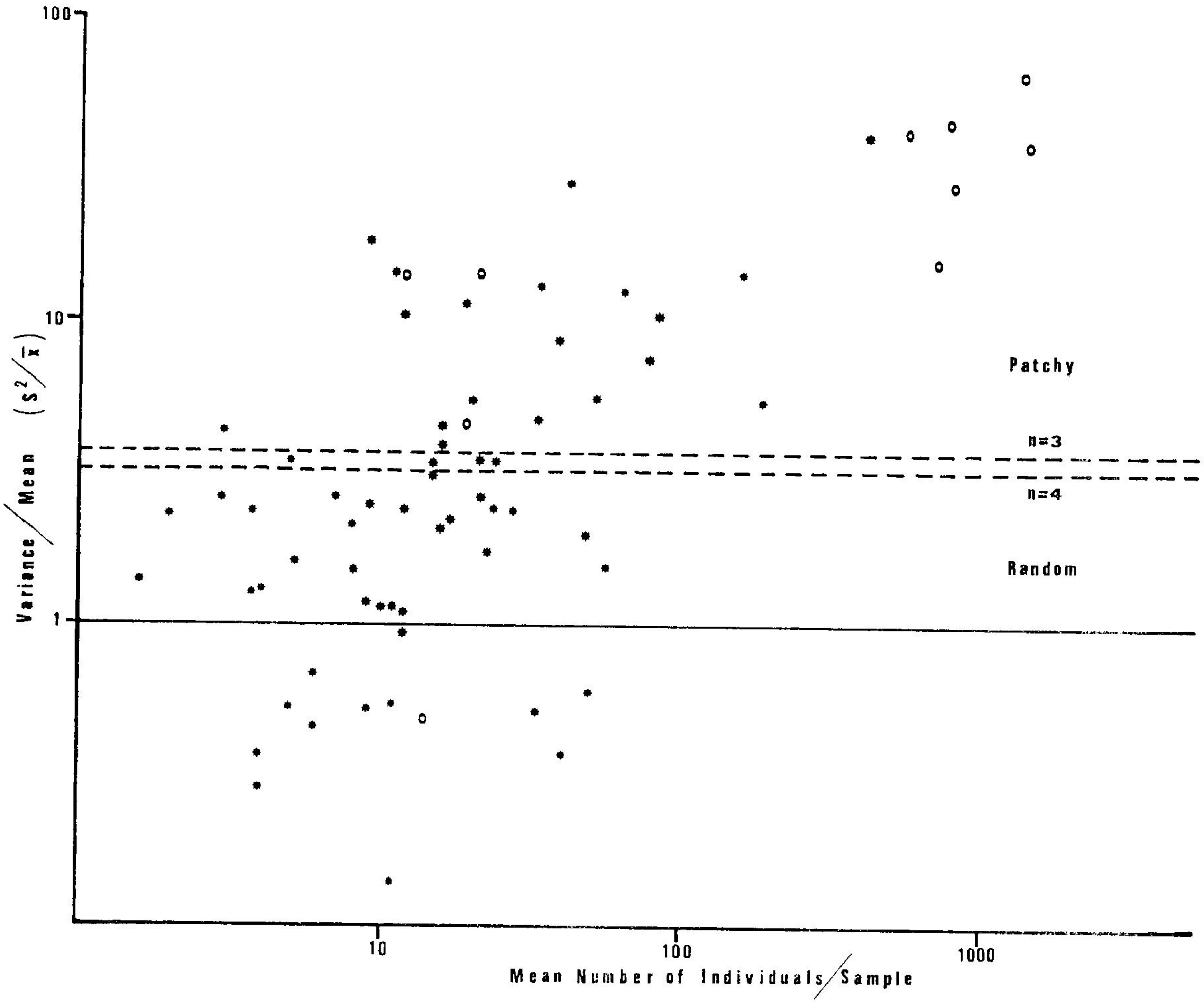
n = number of replicate samples

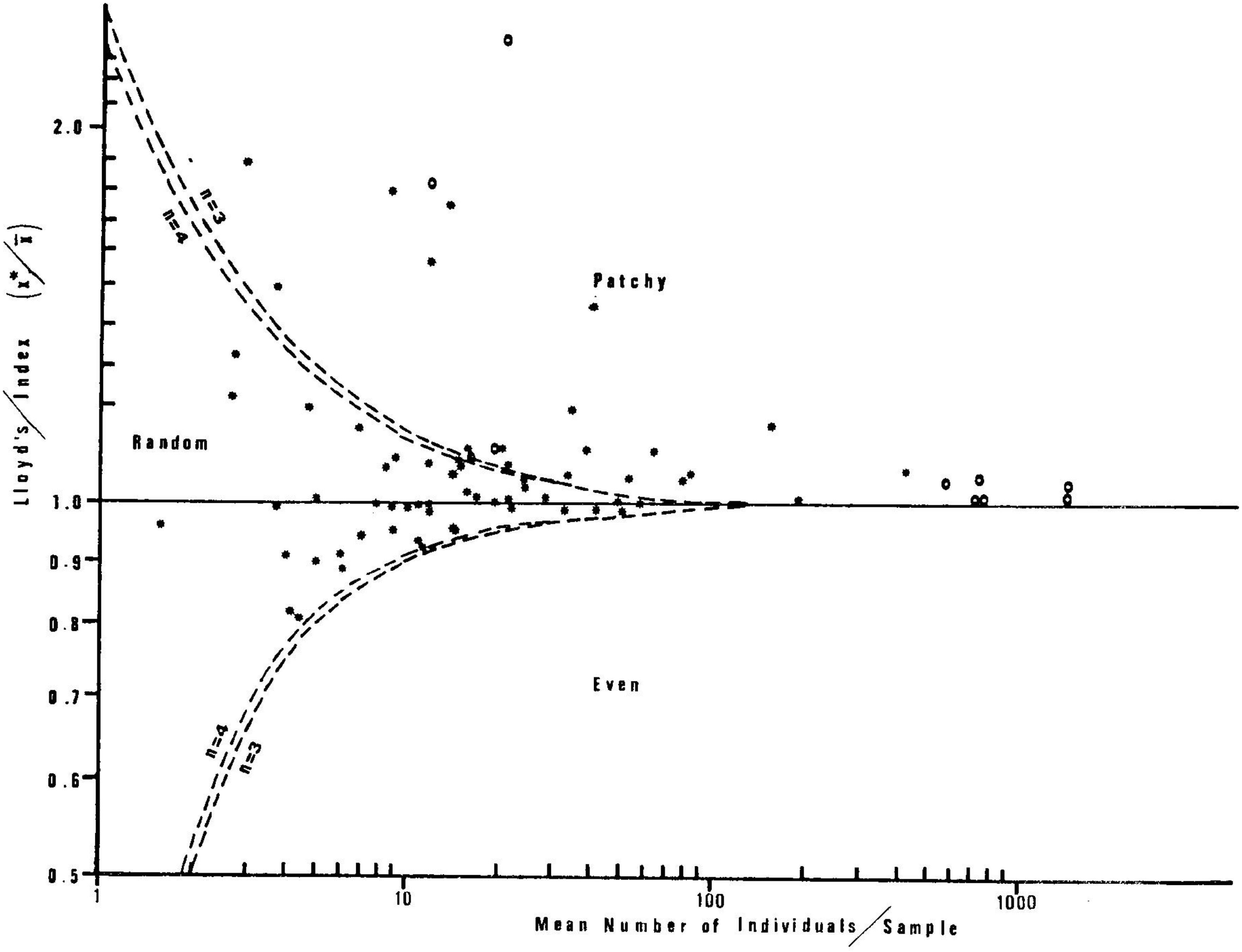
Xi = number of individuals per sample.

In a random distribution, m^* equals m and Lloyd's index is equal to one. Values greater or smaller than unity indicate the presence of an aggregated or even distribution, respectively.

We present variance to mean ratios and Lloyd's indices to patchiness generated by a series of oceanic zooplankton sample sets to illustrate properties of these indices. Samples were taken on alternate days from 30 January to 5 February 1981 at a depth of 20 m from a platform anchored in 1000 m of water off the southeast coast of Puerto Rico (17° 56.3' N, 65° 51.5' W) using an on-deck pumping system. Each sample set consisted of 4 replicates taken approximately at hourly intervals around local noon and midnight, respectively. Samples were filtered through a 202 um mesh net for 8 minutes corresponding to a volume of 5.3 m^3 and preserved in 4% buffered formalin. A total of 3 major groups (total calanoids, cyclopoids and harpacticoids) and 22 copepod species were used in the calculations. Only replicate samples representing whole counts were used in the calculations to eliminate possible complications arising from subsampling error (Venrick 1978). Variance to mean ratios and Lloyd's index of patchiness are based on either 3 or 4 replicates.

Results plotted against mean densities are shown in Figures 1 and 2. For comparative purposes the 95% C.I. distinguishing the type of pattern represented is shown in the figures. Fisher's Index of Dispersion ($X^2_{n-1} = (n-1)S^2/x$) and a formula modified from Morisita (1959) ($F_{\infty}^{n-1}(\alpha) = \frac{(m^*/m)\ N+n-N}{n-1}$) were used in the calculations of the confidence intervals. Results were similar; about 40% of the sample sets were judged aggregated and the remainder not significantly different from random. No examples of even dispersion were noted. With both Lloyd's index and the variance to mean ratio, apparent randomness may result from the inability to statistically differentiate a patchy or even distribution from a random one at low species abundance, a feature previously noted in both indices (Lloyd, 1966 and Wiebe, 1970). This effect is manifested in greater variability in Lloyd's index and lower variance to mean ratios at low densities. As expected, testing showed the variance to mean ratios to be positively correlated with density. The slope of the geometric mean regression (Sokal and Rohlf, 1981) based on log transformed values was not significantly different from 1.0 (95% C.I., 0.78 - 1.14). This suggests that the differences observed in variance to mean ratios among zooplankton samples as a whole can be most simply interpreted as constant multiplicative effects of density changes rather than variation in intensity of pattern. Comparisons of variance to mean ratios among species may require yet undeveloped Model II analysis of covariance techniques (Sokal and Rohlf 1981). More importantly, dependence with mean densities implies that it is inappropriate to compare variance to


100
10
1
Variance/Mean ($S^2/\bar{x}$)
Patchy
n=3
n=4
Random
10
100
1000
Mean Number of Individuals/Sample



2.0
1.0
0.9
0.8
0.7
0.6
0.5
Lloyd's/Index $(x^*/\bar{x})$
1
10
100
1000
Mean Number of Individuals/Sample
Patchy
Random
Even
n=3
n=4
n=4
n=3

mean ratio when the mean densities differ greatly among sample sets.

Because of the unequal variability in the Lloyd's index with respect to mean density, the non-parametric Kendall-tau rank correlation was used to test for relationship between the index and mean abundance per sample. No significant correlation was detected between Lloyd's index and mean density. It appears then that Lloyd's index does provide a measure of the intensity pattern seen in various copepod species that is independent of their mean density, at least within observed range of densities. The individual indices values for patchiness can therefore be compared directly, although some caution may be advisable in cases of low density sets.

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